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Time constraints and trade-offs among parental care behaviours: effects of brood size, sex and loss of mate

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Animals that provide care to their offspring are likely to face time constraints and, consequently, need to trade-off allocations of time among different behavioural activities. Parental allocation of time is often influenced by intrafamilial conflicts including conflicts of interests between parent and offspring and between parents over optimal parental effort. We investigated effects of offspring demand (by manipulating brood size) and loss of mate (by experimental removal of mate) on allocation of time among parental and nonparental behaviours in the burying beetle *Nicrophorus orbicollis*. With increasing offspring demand, allocation of time to parental care occurred at the cost of nonparental behaviours. Time allocation among parental care behaviours changed with offspring demand. Time spent on care behaviours from which offspring benefit simultaneously did not change with increasing offspring demand. In contrast, time spent on care behaviours that offspring receive individually increased with increasing brood size. This suggests that costs for parents and benefits for offspring differ considerably among parental care behaviours. Removal of the mate affected males and females differently. Widowed males increased their effort, whereas widowed females showed no change in their effort. This result suggests that males and females negotiate their parental effort differently, and costs and benefits of parental care differ considerably between the sexes. In general, our study shows a plastic parental response to mate loss and simultaneous change in offspring demand, indicating that parents negotiate parental efforts while considering offspring demands.

All animals face limits to the amount of time and energy available for specific tasks. Constraints therefore play an important role in shaping patterns of animal behaviour (e.g. Sanz et al. 2000; Johansson et al. 2001). This is especially true for animals that care for their offspring. Intrafamilial conflicts between parents and between parent and offspring often influence allocation of time to parental activities (Parker et al. 2002). Theoretical models of biparental care predict that a parent without help (i.e. a uniparental parent) should provide greater parental effort than a parent aided by a mate (i.e. biparental parent), but less than the total effort of two parents working together (Chase 1980; Houston & Davies 1985; Winkler 1987; McNamara et al. 1999). The plasticity in parental behaviour, however, depends on the evolutionary strategy between parents. If the mate of a biparental parent dies or leaves prematurely, the remaining parent should continue providing care at the current level if mates use a 'sealed-bid' strategy (Chase 1980; Houston & Davies 1985; Winkler 1987). Therefore, biparental parents and widowed parents should provide the same amount of parental care and respond similarly to increases in brood size. In contrast, if biparental parents negotiate their parental efforts, the remaining mate should increase its parental effort to compensate for the loss of its mate (McNamara et al. 1999). Yet, the new effort level of the widowed parent should still be lower than the total parental effort of two parents combined (McNamara et al. 1999). When time is limited and brood size increases, widowed parents should, therefore, reach the upper limit of parental effort at a lower brood size than biparental parents.

Theoretically, parental effort should increase with increasing offspring needs (Kilner & Johnstone 1997; Mock & Parker 1997). Assuming that the needs of a brood and

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the signals for need increase with the number of offspring, parental effort should increase with brood size. Such a relationship has been shown by studies manipulating brood size (e.g. Lonzano & Lemon 1998; Siikamäki et al. 1998; Rauter & Moore 1999; Sanz & Tinbergen 1999). In iteroparus animals, a minimal amount of time must be spent on self-maintenance to ensure survival to subsequent breeding attempts (Martins & Wright 1993). Therefore, under time constraints, parental effort should initially increase but eventually level off with increasing brood size. In the presence of time constraints, an increase in parental effort, measured as time spent on parental care, can occur at cost of the time spent on nonparental activities (Martins & Wright 1993; Scott & Gladstein 1993; Whittingham 1993).

Different parental care behaviours differ in their value to offspring. If all offspring share the benefits of a particular parental behaviour equally and simultaneously, the parental care behaviour is predicted to be independent of brood size (Lazarus & Inglis 1986). If benefits of a particular parental care behaviour are divided among offspring and received individually, then the parental care behaviour should increase with brood size (Lazarus & Inglis 1986). Based on these predictions and the considerations above regarding the effect of brood size on parental effort, time spent on parental care that offspring receive individually should first increase and then level off with increasing brood size, if time is limited. Time allocated to parental care behaviours that offspring receive simultaneously, however, should stay constant with increasing brood size despite time constraints.

To investigate effects of offspring demand and loss of mate on allocation of time among parental activities and nonparental behaviours, we simultaneously manipulated brood size and loss of mate in the burying beetle *Nicrophorus orbicollis*. We determined (1) how *N. orbicollis* parents change allocation of time to parental and nonparental behaviours with increasing brood size, (2) how the change of allocation of time is affected by the loss of the mate, and (3) whether there are differences between sexes in how they respond to increase in brood size and loss of the mate. This study was conducted as a companion to our previous work that examined the change in biparental care in relation to changes in brood size and compared offspring solicitation under biparental and uniparental care at constant brood size (Rauter & Moore 1999). In the current study, we are particularly interested in how trade-offs among care and other activities are simultaneously influenced by changes in brood size and removal of the mate.

Burying Beetle Natural History

Burying beetles provide an opportunity to empirically test models of parental care (Rauter & Moore 1999), which is lacking for much of parental care research (Parker et al. 2002). Parental care is well developed in this group, with multiple care behaviours expressed as well as uniparental male, uniparental female and biparental care (Eggert & Müller 1997; Scott 1998).

Burying beetles bury and prepare small dead animals as a food resource for their offspring (Eggert & Müller 1997; Scott 1998). Parent beetles show three parental care behaviours affecting the amount and quality of food resources for larvae. First, parent beetles provision food directly to the larvae by feeding regurgitated carrion. Second, parent beetles produce a crater on top of the carrion in which they release droplets of regurgitated carrion from which the larvae can feed themselves. This behaviour is called processing carrion. Third, the parents maintain the carrion by keeping it moist and free of mould. Previous studies have shown that the three parental care behaviours differ in how brood size or larval begging affects parental response (Rauter & Moore 1999; Smiseth & Moore 2002). Provisioning (i.e. parental care behaviour received individually by offspring) increases with increasing begging or brood size, whereas processing and maintenance of carrion (i.e. parental care behaviour received simultaneously by offspring) is unaffected by brood size or larval begging.

Time spent on parental care affects subsequent reproductive success. High levels of parental care in *N. vespilloides* cause lower brood masses in second broods compared with first broods (Jenkins et al. 2000).

Both parents usually provide care in *N. orbicollis* in nature, but uniparental parents can also be found (Wilson & Fudge 1984). Both males and females are able to perform all parental care behaviours, but in the presence of a mate, males tend to spend less time provisioning food and processing carrion than do females (Fetherston et al. 1990; Rauter & Moore 1999; Smiseth & Moore 2004).

METHODS

Study Animal

All of the beetles used in this study were first-generation offspring of field-caught *N. orbicollis* collected in the Research Forest of Berea College, Kentucky, U.S.A. Before the experiment, the beetles were maintained individually in plastic containers ($15 \times 10 \times 5$ cm) filled two-thirds with moist peat and kept at a temperature of 20–23 °C and under a 15:9 h light:dark cycle. The beetles were fed previously frozen mealworms (*Tenebrio*) ad libitum twice per week.

As nematode load of beetles reared in the laboratory can increase exponentially from one generation to the next, causing reduced larval growth and developmental anomalies during metamorphosis (C. M. Rauter, unpublished data), we reduced the nematode load of wild-caught beetles by transferring the beetles to a new mouse after they had interred the first mouse and eggs had been laid. This procedure reduced nematode load considerably in about half of the first-generation offspring.

Experimental Design

We initiated the experiment by randomly mating 166 virgin male with 166 virgin female beetles. Each pair was placed into a clear plastic container (15 × 10 × 5 cm) with about 2 cm of moist peat and a previously frozen mouse of 30–39 g (supplied from Perfect Pets Inc., Belleville, Michigan, U.S.A.). We collected eggs and handled eggs and newly hatched larvae following the procedure described in Rauter & Moore (1999).

Manipulation of Brood Size and Mate Removal

We manipulated presence or absence of a mate by removing one parent from randomly chosen beetle pairs 12 h after the larvae had been placed upon the carrion. Preliminary observations indicated that widowed male parents deserted the larvae if the female was removed earlier. This procedure allowed us also to control for differences between paired and widowed parents in carrion burying and preparation before larvae were present on the carrion. The experimental removal of mates resulted in 34 female widowed parents, 32 male widowed parents and 26 female and male paired parents. Seventy-four of the original 166 broods were so heavily infested with nematodes that larval development was impaired. We therefore used only nematode-free broods in the analyses.

We manipulated the brood size when the larvae were 1 day old and had moulted to the second instar. The medium brood size (i.e. 15 larvae) in the experiment corresponded to the average brood size reported in earlier studies on *N. orbicollis* (Wilson & Fudge 1984; Scott & Traniello 1990; Trumbo 1991). For small brood size (i.e. 5 larvae), we chose the average brood size minus two times the reported standard deviation (Wilson & Fudge 1984; Scott & Traniello 1990; Trumbo 1991). We chose the average plus two standard deviations as the large brood size (i.e. 25 larvae).

For the first step of the brood size manipulation, we removed the larvae from their parents. Second, we mixed larvae from same-age broods disregarding whether the larvae originated from widowed male, widowed female or biparental broods. Third, we redistributed the larvae randomly among the parents, while adjusting the brood size. We mixed and randomly distributed the larvae to control for genetic correlations between parent and offspring behaviour (Wolf & Brodie 1998; Kölliker et al. 2000; Agrawal et al. 2001; Kölliker & Richner 2001). Fourth, 2 h after placing the larvae back onto the carrion, we observed the care behaviour of the parents. Fifth, after the behavioural observation, the larvae were removed, mixed and redistributed again while adjusting a new brood size for each parent or pair of parents. The parental behaviour was again observed 2 h after brood size adjustment. After the second observation, the whole procedure was repeated a third time for each parent or pair of parents. We manipulated the brood size such that each widowed parent (i.e. widowed male or widowed female parent) or pair of paired parents experienced sequentially three different brood sizes (5 larvae, 15 larvae and 25 larvae). We randomly chose the order of brood sizes for each parent or pair of parents to control for temporal variation in parental care behaviour.

Parental and Nonparental Care Behaviour

Using instantaneous sampling (Martin & Bateson 1993), we recorded parental behaviour every 1 min for 30 min. We scored the following parental care behaviours.

(1) Provisioning to brood: parent regurgitates to larva through mouth-to-mouth contact.

(2) Processing carrion: parent beetle remains stationary in or at the edge of the crater and treats carrion with mouthparts.

(3) Carrion maintenance: parent beetle treats the outside of the mouse carrion with mouthparts while walking or standing, or the parent beetle walks on the outside of the carrion with its abdomen touching the carrion.

(4) Providing parental care: parent beetle either provides food to larvae, processes carrion or maintains carrion.

(5) Nonparental care behaviour in brood chamber: parent beetle does not perform any of the above care behaviours, but is present in the brood chamber.

(6) Absent from brood chamber: parent beetle does not perform any of the above care behaviours and is absent from the brood chamber.

Statistical Analysis

Variables deviating from normal distribution were either subject to arcsine or square-root transformation. The behaviour absent from brood chamber could not be transformed into a normal distribution and was reduced to a binomial variable (i.e. present in the brood chamber or absent from the brood chamber). We analysed the data with a repeated measures ANOVA (Winer et al. 1991) with one within-factor (brood size) and two grouping factors (mate: present or removed; sex of parent: male or female). We tested our prediction of brood size effects on parental care behaviours using a priori contrasts between small and medium-sized broods and between medium-sized and large broods. We analysed our data with SAS version 8.2 (SAS Institute 2001).

Observations of males and females within a biparental pair were assumed to be independent, although the pair cared for the same larvae. To examine the extent of the independence, for each pair of parents, we calculated the correlation between male and female behaviour for all parental care behaviours (providing parental care, provisioning, processing carrion and carrion maintenance). Of the resulting 104 correlations, 100 were nonsignificant, suggesting that we were justified in treating observations of males and females within a pair as independent observations.

RESULTS

Time Spent Providing Parental Care

The repeated measures ANOVA, with mate removal and caretaker sex as factors plus brood size as a repeated factor, provided two pieces of information: how groups differed (‘between parents’ variation) and how individuals changed (‘within parents’ variation). In general, all parents spent a substantial amount of time providing

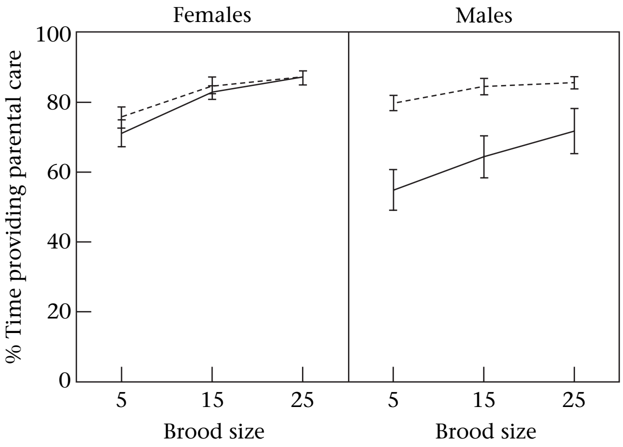

Figure 1. Time spent providing parental care in relation to brood size (number of larvae) for females and males in the presence (solid line) and absence of a mate (dashed line). Mean ± SE are shown.

parental care (Fig. 1). Between parents, removal of mate had a significant effect on the amount of time spent providing care, whereas the effect of caretaker sex approached significance (Table 1). Widowed parents spent more time providing care than paired parents. Females showed a nonsignificant tendency to spend more time on parental care than did males (Fig. 1). Males and females, however, differed significantly in the degree of their response, depending on whether a mate was present or not (significant mate∗sex interaction; Table 1). Paired males spent much less time providing care than widowed males, whereas widowed females spent almost the same amount of time providing care as paired females.

Within-parent analyses showed that individual parental care increased asymptotically with brood size (5 larvae versus 15 larvae: $F_{1,114} = 23.57$, $P < 0.0001$; 15 larvae versus 25 larvae: $F_{1,114} = 5.36$, $P = 0.022$, not significant after Bonferroni correction; Table 1, Fig. 1). None of the interactions with brood size was significant (Table 1).

On a per-larva basis, however, within-parent analyses showed that parental care decreased continuously with brood size (brood size: $F_{2,228} = 509.27$, $P < 0.0001$; 5 larvae versus 15 larvae: $F_{1,114} = 417.79$, $P < 0.0001$; 15 larvae versus 25 larvae: $F_{1,114} = 206.97$, $P < 0.0001$). Widowed parents provided more care per larva than paired parents at all brood sizes (brood size∗mate: $F_{2,228} = 11.91$, $P = 0.0003$; 5 larvae versus 15 larvae: $F_{1,114} = 8.90$, $P = 0.004$; 15 larvae versus 25 larvae: $F_{1,114} = 8.04$, $P = 0.005$).

Time Spent Provisioning Brood

Between parents, none of the factors or their interactions had a significant influence on time spent provisioning food to brood (Table 1, Fig. 2).

Within parents, there was significant variation in time spent provisioning food. Provisioning increased with increasing brood size (5 larvae versus 15 larvae: $F_{1,114} = 44.13$, $P < 0.0001$; 15 larvae versus 25 larvae: $F_{1,114} = 12.10$, $P = 0.0007$; Table 1). In addition, widowed and paired parents differed in their response to increasing brood size (Table 1, Fig. 2). Both widowed and paired parents increased time spent provisioning when brood size increased from five to 15 larvae ($F_{1,114} = 0.40$, $P = 0.53$), but only biparental parents increased time spent provisioning further when brood size increased from 15 to 25 larvae ($F_{1,114} = 12.14$, $P = 0.0007$). Brood size∗caretaker sex, and the three-way interaction between brood size, caretaker sex and mate removal were not significant influences on variation of provisioning within broods.

Despite an increase of provisioning with increasing brood size, provisioning per larva decreased continuously with increasing brood size (brood size: $F_{2,228} = 160.91$, $P < 0.0001$; 5 larvae versus 15 larvae: $F_{1,114} = 120.73$, $P < 0.0001$; 15 larvae versus 25 larvae: $F_{1,114} = 100.49$, $P < 0.0001$). Widowed parents and paired parents did not differ in their response to an increase in brood size from five to 15 larvae ($F_{1,114} = 6.58$, $P = 0.01$, not significant after Bonferroni correction). Yet, with an increase of brood size from 15 to 25 larvae, widowed parents reduced provisioning per larva less than paired parents ($F_{1,114} = 12.91$, $P = 0.0005$).

Table 1. Repeated measures ANOVA examining the effect of a mate (present or removed), caretaker sex (male or female) and repeated manipulation of brood size (5, 15 and 25 larvae) on time spent providing parental care, provisioning, processing carrion and carrion maintenance

		Providing parental care		Provisioning		Processing carrion		Carrion maintenance	
Source	df	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Between parents									
Mate	1	15.26	0.0002**	2.99	0.09	3.49	0.06	13.97	0.0003**
Sex	1	6.91	0.010*	2.71	0.10	4.37	0.04	0.29	0.59
Mate∗sex	1	7.24	0.008**	2.24	0.14	5.95	0.02	1.46	0.23
Error	114								
Within parents									
Brood size	2	27.37	<0.0001**	50.06	<0.0001**	1.97	0.14	5.51	0.005**
Brood size∗mate	2	2.97	0.054	7.59	0.0006**	0.92	0.40	0.03	0.97
Brood size∗sex	2	0.42	0.66	2.41	0.09	0.80	0.45	0.15	0.86
Brood size∗sex∗mate	2	0.69	0.50	0.88	0.42	0.71	0.49	0.19	0.83
Error	228								

*$P = 0.06$; **$P \leq 0.05$ after applying Bonferroni correction (Hochberg 1988) to control for multiple tests.

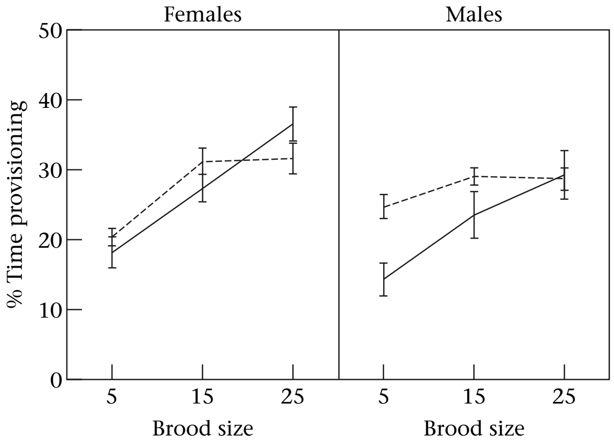

Figure 2. Time spent provisioning food to the brood in relation to brood size (number of larvae) for females and males in the presence (solid line) and absence of a mate (dashed line). Mean ± SE are shown.

Time Spent Processing Carrion

Both between parents and within parents, none of the factors or their interactions significantly influenced the time spent processing carrion (Table 1, Fig. 3).

Time Spent on Carrion Maintenance

There was only one significant factor explaining variation between parents. Removal of mate had a significant effect on time spent on carrion maintenance, with widowed parents spending more time maintaining carrion than paired parents (Table 1, Fig. 4).

There was also only a single factor that explained variation within parents (Table 1). Time spent on carrion maintenance increased when brood size increased from five to 15 larvae ($F_{1,114} = 3.81$, $P = 0.05$), but levelled off when brood size increased from 15 to 25 larvae ($F_{1,114} = 1.89$, $P = 0.17$; Fig. 4). None of the interactions was significant.

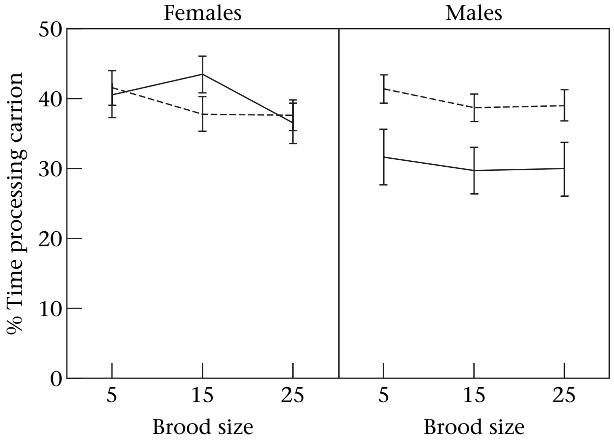

Figure 3. Time spent processing carrion in relation to brood size (number of larvae) for females and males in the presence (solid line) and absence of a mate (dashed line). Mean ± SE are shown.

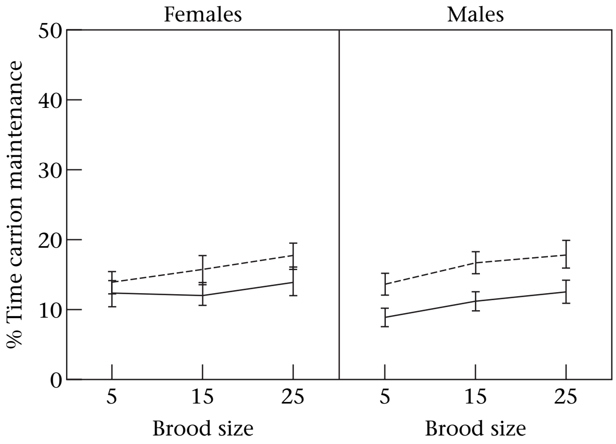

Figure 4. Time spent on carrion maintenance in relation to brood size (number of larvae) for females and males in the presence (solid line) and absence of a mate (dashed line). Mean ± SE are shown.

Nonparental Care Behaviours

None of the factors had a significant effect on variation between parents in time spent on nonparental care behaviours in the brood chamber (Table 2). The only significant effect on variation within parents in nonparental behaviours within the brood chamber was brood size (Table 2). Time allocated to nonparental behaviours decreased as brood size increased from small to medium ($F_{1,114} = 19.78$, $P < 0.0001$) and did not change with a further increase of brood size ($F_{1,114} = 0.50$, $P = 0.48$; Fig. 5).

Between parents, the effect of mate removal on absence from the brood chamber approached significance (Table 2). There was also a greater tendency for paired parents to be absent from the brood chamber compared with widowed parents (Table 2, Fig. 6). Neither caretaker sex nor the

Table 2. Repeated measures ANOVA examining the effect of mate (present or removed), caretaker sex (male or female) and repeated manipulation of brood size (5, 15 and 25 larvae) on time spent on 'nonparental behaviours in the brood chamber' and 'absent from the brood chamber' (absent from brood chamber at least once = 1; never absent from brood chamber = 0)

		Nonparental care		Absent from brood chamber	
Source	df	*F*	*P*	*F*	*P*
Between parents					
Mate	1	0.04	0.84	6.41	0.01*
Sex	1	0.00	0.97	1.79	0.18
Mate∗sex	1	0.90	0.34	0.58	0.45
Error	114				
Within parents					
Brood size	2	16.26	<0.0001**	7.79	0.0005**
Brood size∗mate	2	1.04	0.35	1.72	0.18
Brood size∗sex	2	0.22	0.80	0.98	0.38
Brood size∗ sex∗mate	2	0.64	0.53	0.28	0.76
Error	228				

*$P = 0.06$; **$P \leq 0.05$ after applying Bonferroni correction (Hochberg 1988) to control for multiple tests.

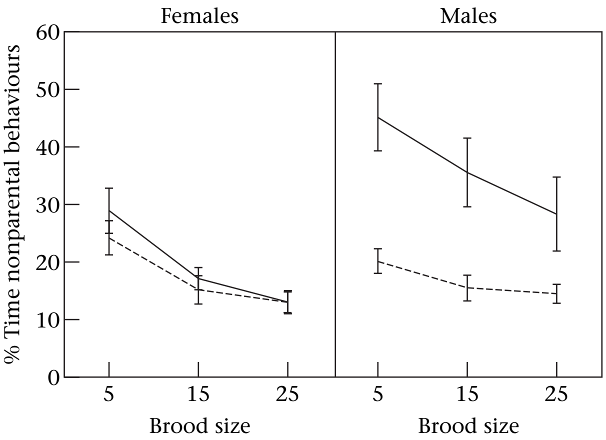

Figure 5. Time spent on nonparental behaviours in the brood chamber in relation to brood size (number of larvae) for females and males in the presence (solid line) and absence of a mate (dashed line). Mean ± SE are shown.

interaction between caretaker sex and mate removal significantly influenced absence from the brood chamber. Brood size significantly influenced within-brood variation in absence from the brood chamber (Table 2). Parents with small and medium-sized broods did not differ in absence from the brood chamber ($F_{1,114} = 2.46$, $P = 0.12$; Fig. 6), but parents with large broods tended to be absent from the brood chamber less often than parents of medium-sized broods ($F_{1,114} = 6.43$, $P = 0.01$, $P = 0.06$ after Bonferroni correction). None of the interactions between the other factors and brood size influenced within-brood variation.

DISCUSSION

We found that the sexes differed in their responses to our manipulations. Males reduced parental care drastically in the presence of a mate, whereas paired females showed the same amount of parental care as widowed females. Overall, with increasing offspring demand, parent beetles devoted more time to parental care and less time to nonparental activities. Thus, allocation of time among parental care behaviours changed with increasing offspring demand. Even though time spent providing care increased with increasing brood size, care per larva decreased with increasing brood size. In addition, parental care behaviour changed more when broods increased from five to 15 larvae than when brood size increased from 15 to 25 larvae, suggesting that widowed females, widowed males and paired females were working at their maximum for parental activities. Nevertheless, not all behaviours changed equally. Whereas time spent on processing carrion and carrion maintenance did not change or increased only slightly, respectively, with increasing offspring demand, time allocated to provisioning food increased considerably. Widowed parents increased time provisioning food asymptotically with increasing offspring demand, whereas paired parents showed a continuous increase. Widowed parents spent more time providing care and maintaining carrion than biparental parents.

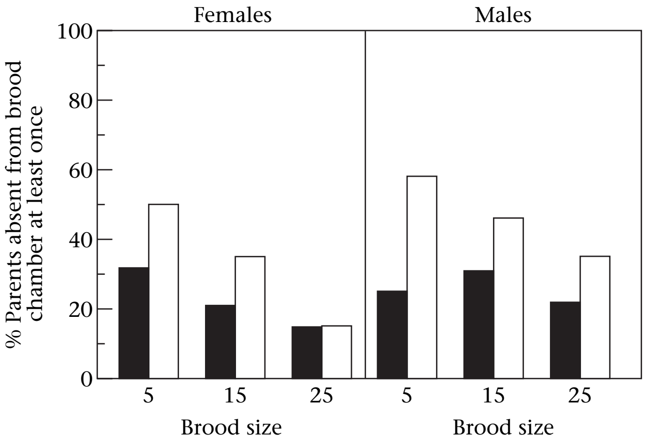

Figure 6. Percentage of parents that were absent from the brood chamber at least once (out of 30 scans) in relation to brood size (number of larvae) for females and males in the absence (■) and presence (□) of a mate.

Effects of Mate Removal and Caretaker Sex

In the presence of a mate, males provided less parental care than females. This is consistent with previous findings for *N. orbicollis* (Fetherston et al. 1990) and for *N. vespilloides* (Smiseth & Moore 2004; P. T. Smiseth, C. J. Dawson, E. Varley & A. J. Moore, unpublished data). The sex difference in parental effort of widowed parents compared with that of paired parents suggests that males and females differ in their compensation strategies. This contradicts the interpretation by Fetherston et al. (1994) regarding compensation but parallels the results found by Smiseth & Moore (2004) for *N. vespilloides*. Our results are also identical to the repeated-measures manipulation of P. T. Smiseth, C. J. Dawson, E. Varley & A. J. Moore (unpublished data), who compared behaviour before and after removal of a parent but did not manipulate brood size.

The differences in compensation strategies between the sexes may be due to differences in costs and benefits of parental care. Males may encounter higher costs of parental care, as they may miss opportunities for additional matings. Benefits of care may be higher for females. Females seem to gain personal benefits when providing care, because single females increase brood size from first to second broods (P. T. Smiseth et al., unpublished data).

Allocation of Time to Parental and Nonparental Behaviour

The asymptotical increase in time spent providing parental care and time provisioning food with increasing offspring demand suggests that parent–offspring conflict increases with increasing brood size. Parents appear to be working at their maximum (either that they are willing or able to provide), and the amount of care provided per offspring is less in large broods than in small broods. The evolutionary importance of this conflict depends on the fitness effects for offspring (Parker et al. 2002; Royle et al. 2002). The sex differences in response to mate loss suggests that the time constraints differ for males and females in the presence of a mate, and therefore, sexual conflict is likely to be important as well.

Although time spent providing parental care and provisioning food increased with increasing brood size, time spent per larva also decreased, indicating incomplete compensation. Widowed parents spent more time providing care and provisioning food per larva than paired parents, yet they still spent less time than two parents together. Lower provisioning rates of widowed parents may slow down larval growth and increase larval development time, as has been observed for larvae reared without parental care compared with larvae reared by single females (Rauter & Moore 2002; Smiseth & Moore 2003). Differences in growth patterns between larvae reared by widowed parents and larvae reared by two parents may explain why studies comparing final larval mass between widowed and biparental broods did not find any differences (Eggert & Müller 1997; Scott 1998; P. T. Smiseth et al., unpublished data).

The different responses seen in the three parental care behaviours with increasing brood size are similar to the parental response to increases in brood size in *N. vespilloides* (Smiseth & Moore 2002, 2004). This supports the idea that parental care behaviours differ in costs for parents and benefits for offspring. Provisioning is likely to have greater benefits than processing or maintaining the carrion. Thus, there can be trade-offs between different behaviours, and conflicts between the sexes and between parents and offspring will depend on the behaviour examined.

In general, our results show a plastic response of parents to loss of mate and simultaneous change in offspring demand, manipulated by changing brood size. These results support different aspects of biparental care models (McNamara et al. 1999; Parker et al. 2002): one parent provides less care than two, but males compensate for the loss of a mate whereas females do not change their parental effort. An implicit assumption of biparental care models, however, is that offspring demand is fixed. This applies only for parental care behaviours from which offspring benefit simultaneously. If offspring profit from parental care behaviours individually, the outcome of the negotiations between the parents depends on the offspring demands. Our work shows that parental care can also depend on offspring need, and as suggested by Parker et al. (2002), there is an interplay of conflicts between the two parents and between parents and their offspring. Future models of biparental care involving negotiations between parents should therefore incorporate a state-dependent variable representing offspring demand.

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